

Adaptation of gender derived from biological motion

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Human observers adapted to complex biological motions that distinguish males from females: viewing the gait of one gender biased judgments of subsequent gaits toward the opposite gender. This adaptation was not simply due to local features of the stimuli but instead relied upon the global motion of the figures. These results suggest the existence of neurons selective for gender and demonstrate that gender-from-motion judgments are not fixed but depend upon recent viewing history.

Prolonged viewing of elementary visual features such as color, motion and orientation can result in systematic shifts in the perception of subsequent stimuli¹. For example, viewing a stimulus moving in one direction results in subsequent ambiguous stimuli appearing to move in the opposite direction², a manifestation of motion adaptation. Adaptation effects are thought to imply the existence of neurons selective for the adapted feature³, which is supported by the fact that adaptation effects for basic features parallel the established selectivities of single neurons within individual early visual areas. Application of adaptation techniques to understand the neural representation of higher-order features, such as the identity⁴ or gender of a human⁵, is more problematic. These features might either be represented implicitly by a network of neurons, each selective for the different

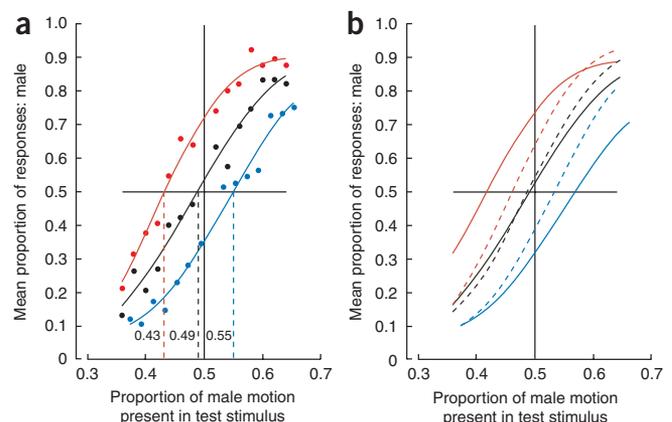
constitutive lower-order features, or by single neurons selective for that higher-order feature—for example, face neurons^{6,7}. Accordingly, to provide evidence of neurons selective for a higher-order feature, one must demonstrate that adaptation to that feature cannot be accounted for by adaptation to constitutive lower-order features.

Human observers can readily identify the gender of a human walk, even when the only visible information comes from lights attached to the major joints of the body^{8,9} (point light walker, PLWer¹⁰). As no single light alone conveys sufficient information¹¹, this gender discrimination requires the integration of local information into a global percept. If prolonged viewing of PLWers was found to produce systematic shifts in gender discrimination of subsequent ambiguous stimuli, this would provide evidence of gender-specific adaptation. Specifically, viewing a female PLWer should increase the probability of judging a subsequent ambiguous PLWer as male, and vice versa.

On each trial, observers, who had given written informed consent, watched an adapting PLWer for 11.67 s. These adapters depicted the gait of a male, a female or an ambiguous walker (proportion 0.5 male, 0.5 female; **Supplementary Methods** online). After a brief blank interval, a test PLWer was presented for 1 s (~0.5 of a gait cycle) and observers reported the perceived gender: male or female. Randomly interleaving the three adapting conditions ensured that the observers' average adaptation state would be neutral. Test PLWers were generated by morphing the male and female prototypes in varying proportions. All PLWers were shown in frontal profile to maximize the lateral sway cues mediating gender discrimination¹¹.

To quantify performance (**Fig. 1a**), we determined the 'ambiguity point' (AP): the proportion of maleness in the test stimuli yielding male and female reports with equal probability. Critically, APs differed reliably across adapting conditions ($F_{2,12} = 10.452$, $P = 0.002$). The AP for neutral adapters (0.49) revealed a perceptual gender boundary that closely matched the physical male-female boundary. However,

Figure 1 Gender discrimination performance after viewing male (blue), female (red) and gender-neutral (black) PLWers. Curves were fitted with cumulative Gaussians, with base and maximal values as free parameters. The 'ambiguity point' (AP)—that is, the male/female proportion judged to be male half the time—allowed comparison across adaptation conditions. **(a)** APs for test stimuli following neutral (mean \pm s.e.m. = 0.49 ± 0.02), female (0.43 ± 0.04) and male (0.55 ± 0.07) adapters. The neutral AP was not different from the ideal 0.5 level ($t_5 = -0.92$, $P = 0.398$). $n = 7$ subjects; 6 naïve, 1 author (H.J.); 5 female. **(b)** APs for test stimuli following adaptation by coherent (solid lines) PLWers (neutral = 0.49 ± 0.05 ; female = 0.42 ± 0.04 ; male = 0.57 ± 0.05) and dephased (dashed lines) versions (neutral = 0.49 ± 0.05 ; female = 0.46 ± 0.01 ; male = 0.53 ± 0.04). For coherent adapters, reliable differences were observed between the neutral and the female (-0.07 , $t_5 = 3.51$, $P = 0.017$) and between the neutral and the male ($+0.08$, $t_5 = 5.56$, $P < 0.003$) adapters. In the dephased version, however, no reliable difference was observed between neutral and male adapter conditions ($+0.04$, $t_5 = 2.54$, $P = 0.06$), nor between the neutral and female conditions (-0.03 , $t_5 = -1.60$, $P = 0.169$). Neither coherent nor dephased neutral adapters yielded APs that were statistically different from 0.5 ($t_5 < 1$, $P > 0.6$). $n = 6$ subjects; 5 naïve, 1 author (M.F.); 3 female.



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relative to that neutral condition, APs were significantly shifted for both female (-0.06 , Bonferroni planned contrast, $P < 0.05$) and male ($+0.06$, $P < 0.05$) adapters. Consistent with gender adaptation, viewing male and female PLWers systematically shifted the observers' perception of test stimuli toward the opposite gender. There was no evidence of changes in sensitivity across the adapter conditions as measured by the slopes of the curves at the AP point ($F_{2,12} < 1$, $P > 0.4$).

Do these results truly reflect adaptation to gender from biological motion or simply low-level adaptation to the local motion of individual lights? To answer this, we created dephased adapters by randomizing the gait cycle phases of individual lights in the original coherent adapters. This disrupted global coherence but left the local motion of each light unchanged. A new group of subjects completed coherent and dephased versions of the task (**Fig. 1b**). Reliable evidence for gender-specific adaptation was again observed in the coherent adapter condition ($F_{2,10} = 24.58$, $P < 0.001$). If adaptation was solely due to local motion, coherent and dephased adapters should be equally effective. This was not the case: although a reliable adaptation effect still occurred for the dephased adapters ($F_{2,10} = 8.285$, $P = 0.008$), it was significantly reduced relative to the coherent versions ($F_{2,10} = 12.095$, $P = 0.002$). The reduced adaptation effect observed with the dephased stimuli reflects the loss of the contribution of gender derived from biological motion.

The dephased stimuli control for local motion. The reduced adaptation effect observed with those stimuli must therefore reflect the loss of the contribution of gender derived from biological motion. The residual effect seen with dephased stimuli may reflect the contribution of low-level mechanisms. However, the residual adaptation effect seen for our dephased stimuli does not actually define the contribution of low-level adaptation, but rather sets an upper bound on that contribution. As can be seen from the example stimuli (**Supplementary Videos 1–3** online), dephasing PLWers greatly impairs gender identity but does not destroy it. Thus, the small adaptation effect seen with dephased PLWers may plausibly be due to other aspects of the stimuli that contribute to gender identity.

Our findings demonstrate that gender identification of human walkers is rapidly malleable and subject to adaptation. Adaptation of low-level features was found to be insufficient to account for the observed changes in gender discrimination. We conclude that our results reflect adaptation occurring after the level of local motion processing. These findings are consistent with the existence of neurons selective for gender, as derived from biological motion. Such neurons

might reside in cortical areas previously identified as gender-related¹². However, as suggested by the McCullough and other contingent after-effects, adaptation may occur across a network of neurons that represent the compound stimuli¹³. Whether gender adaptation is subserved by individual neurons tuned for gender or by a network of neurons awaits future experimentation. Given that adaptation methods coupled with functional magnetic resonance imaging (fMRI) have proven a successful tool for the investigation of low-level neuronal selectivity (for example, refs. 14,15), our study points the way toward extending that approach to the noninvasive study of the neuronal mechanisms subserving the processing of gender information.

Note: Supplementary information is available on the Nature Neuroscience website.

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AUTHOR CONTRIBUTIONS

H.J. designed and conducted the experiment, constructed the stimuli, analyzed the data and contributed to discussions and writing the manuscript. M.F. contributed to discussions and writing the manuscript. G.R.S. had the original experimental idea, contributed to discussions and writing the manuscript.

COMPETING INTERESTS STATEMENT

The authors declare that they have no competing financial interests.

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